A PLEISTOCENE LONGIROSTRINE CROCODILIAN FROM RIVERSLEIGH: FIRST FOSSIL OCCURRENCE OF CROCODYLUS JOHNSTONI KREFFT

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Willis, P.M.A. and Archer, M. 1990 3 31: A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. *Mem. Qd Mus.* 28(1): 159–163. Brisbane. ISSN 0079–8835.

A dentary of a longirostrine crocodile, recovered from Pleistocene deposits on Riversleigh Station, northwestern Queensland, represents the first fossil occurrence and the oldest record of *Crocodylus johnstoni*. The age of this specimen and its geographic location are consistent with the hypothesis that *C. johnstoni* evolved from a more generalised, saltwater-tolerant species some time after the Pliocene.

☐ *Crocodilia, Crocodylus, Pleistocene, Australia.*

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A longirostrine crocodilian dentary was collected from Pleistocene deposits on Riversleigh Station by members of the University of New South Wales 1986 Riversleigh Expedition. It is described here in detail because, although it appears to be referable to *Crocodylus johnstoni*, it displays several features that invite broader comparisons bearing on the affinities of this species. QM = Queensland Museum.

Material

QM F13115, an incomplete left dentary, with four teeth (Fig. 1).

Locality and Sediments

"Terrace Site", the source locality, is a perched and dissected river-terrace deposit 5 km downstream from the crossing of the Gregory River and the Lawn Hill road, along the west bank of the Gregory River, Riversleigh Station, northwestern Queensland. More precise locality data are available on application to the Queensland Museum or the University of New South Wales. The unnamed deposits at this site are fluviatile sediments, mostly unconsolidated sands, clays and conglomerates which are locally indurated by a light carbonate cement.

Associated Fauna

The "Terrace Site" material is referred to the Terrace Site Local Fauna (Archer *et al.* 1989). Aside from the crocodilian described here, other taxa in this fauna include: *Diprotodon optatum*, unidentified macropodids, an unidentified rodent, a varanid, another crocodilian, a large elseyan turtle and freshwater molluscs.

Age

The "Terrace Site" at Riversleigh is considered to be Pleistocene in age because it contains premolars and molars of *Diprotodon optatum*, a species which is unrecorded from pre-Pleistocene deposits (Archer, 1984). Charcoal and shell suitable for radiocarbon dating were retrieved from the level containing QM F13115 but these have not yet been dated.

Description

QM F13115 is an almost complete left dentary of a longirostrine crocodilian (Fig. 1). It is crushed and incomplete posteriorly, and the anterior part of the symphysis is also missing. Although the dentary fragment is large (183 mm long), it is slender and gracile in form. The mandibular symphysis extends to the level of the sixth tooth, while the splenial contact extends to the level of the seventh tooth and thus does not participate in the symphysis. The surface of the dentary is lightly sculptured with indistinct pits.

Fourteen alveoli are preserved but more may have been present further back in the missing portion of the dentary. The buccal rim of the tooth row undulates, but only very slightly. All alveoli are similar in size and round in cross-section. The fourth, ninth and tenth teeth are preserved *in situ*, and an unerupted tooth was recovered from the fifth alveolus. These teeth are slender, with weak

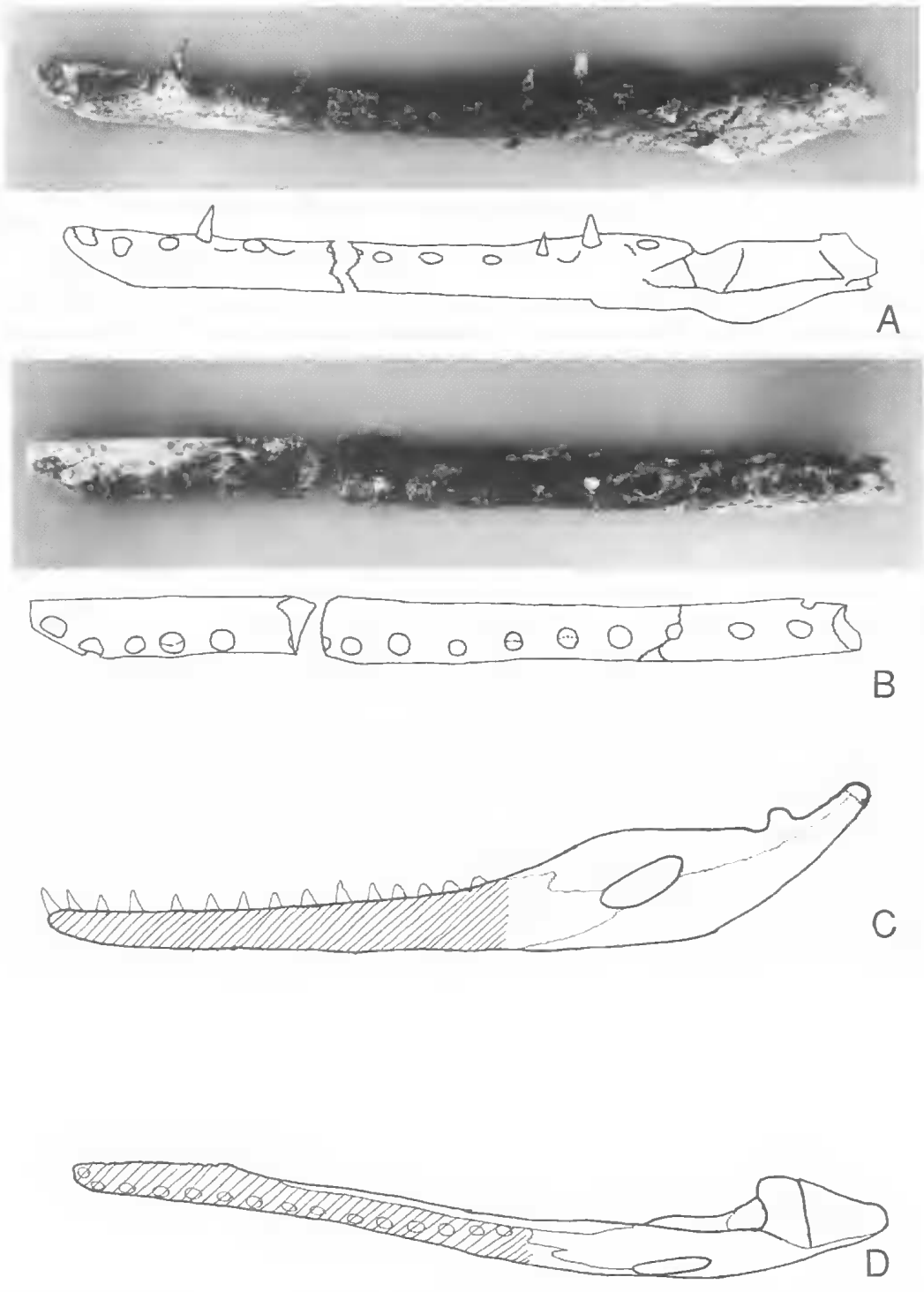

FIG. 1. QM F13115, left dentary of *Crocodylus johnstoni:* a, lateral view; b, dorsal view. Overall length 183 mm. Line drawing reconstructions shown under each view. The left mandible of *C. johnstoni*: c, lateral view; d, dorsal view. Hatching shows portion represented by QM F13115.

anterior and posterior carinae and are striated parallel to the long axis of the crown.

COMPARISONS

Although QM F13115 was initially compared with material or descriptions of all crocodilians, detailed comparisons were eventually narrowed down to specimens of *Crocodylus porosus*, *C. johnstoni* and *C. novaeguineae*. These are the only species that bear close resemblance to this Riversleigh crocodile and the only crocodiles that still survive in the region.

The slender, gracile form of QM F13115 is unlike the heavy, robust dentaries seen in undescribed Miocene crocodilians from Riversleigh and in *Pallimnarchus pollens* (Molnar, 1982a). The dentary of *Quinkana fortirostrum* (Molnar, 1981) is not known, but one would expect a more heavily built, broader dentary for this species than QM F13115. *Pallimnarchus* and *Quinkana* are the only late Cainozoic fossil crocodilians described from Australia. In its overall form, the orientation of the alveoli and the length of the mandibular symphysis the Riversleigh form is clearly different from *'Gavialis' papuensis* (Molnar, 1982b) from Woodlark Island.

QM F13115 is more gracile than the dentary of a similar-sized *C. porosus*. The shape and almost uniform size of the teeth, the barely-undulating tooth row and the narrowness of the dentary distinguish QM F13115 from both *C. porosus* and *C. novaeguineae*.

QM F13115 is indistinguishable from *C. johnstoni* in all features except three: 1, it represents an individual that would be unusually large for this species; 2, the dentary appears to be relatively narrower than that of *C. johnstoni*; and 3, there is a large gap between the fifth and sixth alveoli, not seen in *C. johnstoni*.

Although QM F13115 would represent a very large specimen of *C. johnstoni*, a *t*-test indicates that it is not significantly larger than a sample of *C. johnstoni* (n = 17, mean = 116.1, sd = 35.8, P 0.05). The *t*-test did, however, indicate that QM F13115 probably approaches the predicted extreme in size for this species. No modern specimen known to us exceeds this fossil in size. Presuming that it represents *C. johnstoni*, there are two possible explanations for the large size of QM F13115. First, crocodiles have for some time been hunted for their skins, large specimens being the most intensely sought. Because of this, awareness of the pre-European size range of the freshwater crocodile (and that of most specimens available for study) may be misleadingly low.

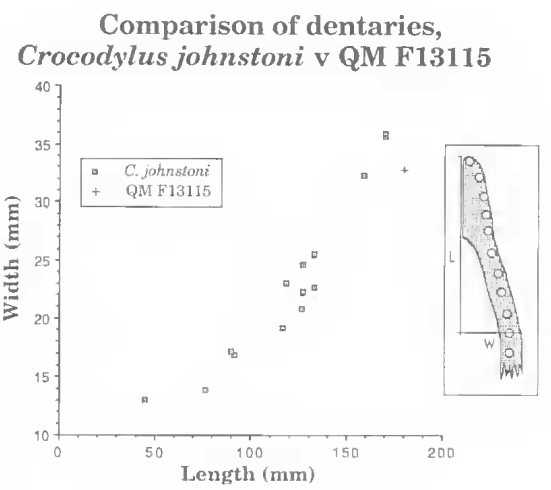

FIG. 2. Length to width ratios of *Crocodylus johnstoni* dentaries. Inset shows measurements on a typical right jaw of *C. johnstoni*. All measurements in mm. Length is measured from the anterior tip along the midline to the level of the tenth tooth; width is measured from the tenth tooth to the midline. These arbitrary measurements are necessary because QM F13115 is distorted posterior to the tenth tooth. Open circle indicates QM F13115; crosses indicate comparative examples of *C. johnstoni*.

A second possible explanation for the large size of QM F13115 involves the hypothetical evolutionary history of the species. It has been suggested by Longman (1925) that *Crocodylus johnstoni* probably descended from a larger, brevirostrine species such as *C. porosus*. Ancestral *C. johnstoni* might then be expected to have been, on average, larger than modern individuals.

The apparent narrowness of the dentary of QM F13115 may be an illusion resulting from its large size. Figure 2 shows that the dentary of modern *C. johnstoni* has a length to width ratio that follows a linear relationship (length = 5.52 width, n = 17, mean = 5.52, sd = 0.46). QM F13115 has a length to width ratio of 5.5. A *t*-test reveals that QM F13115 is not significantly different in this measurement from the comparative sample (P 0.05). Although a non-linear relationship between the length and width of the dentary may exist, the sample size of modern *C. johnstoni* is too small to detect such a relationship.

The large gap between the fifth and sixth alveoli may be nothing more than individual variation and cannot be presumed to have taxonomic or phylogenetic significance. Iordansky (1973) noted

that irregular positioning of teeth is a common anomaly in many crocodilian species.

In summary, the three features in which QM F13115 appears to differ from *C. johnstoni* are not sufficient grounds for recognizing this specimen as a different species.

DISCUSSION

As the first known fossil of *Crocodylus johnstoni*, QM F13115 establishes a minimum age for the species, which Longman (1925) suggested had evolved in northern Australia from more generalised crocodiles. The freshwater habitat of this species restricts its distribution, which is currently limited to the Australian mainland. Salt-tolerance studies of crocodilians (e.g. Taplin, 1984) indicate that some species of crocodilians have a much greater tolerance for salt water than others. This fact, coupled with interpretations of phylogenetic divergence sequences based on studies of blood proteins (Densmore, 1981; Densmore & Dessauer, 1982), prompts the following model as an explanation for the evolutionary history of the genus *Crocodylus* in Australia. By at least Pliocene times, a generalised, salt-water tolerant, ancestral species such as *C. porosus* or *C. acutus* may have dispersed across ocean barriers to estuarine habitats around the world. Some of its descendants subsequently invaded freshwater habitats and speciated into forms intolerant of saltwater, including *C. johnstoni*.

Chronologically the Riversleigh specimen is within the time framework established by protein divergence studies suggesting that *C. johnstoni* and *C. porosus* have diverged since Pliocene time. The large size of the specimen described here is consistent with descent from a larger form like *C. porosus*. Molnar (1979) has described, as *C. porosus*, an early Pliocene crocodile from the freshwater sediments of the Allingham Formation of northeastern Queensland (Archer & Wade, 1976). Clearly *C. porosus* was in Australian freshwater habitats early enough to have given rise to the freshwater crocodile, *Crocodylus johnstoni*.

ACKNOWLEDGEMENTS

We wish to acknowledge the vital financial support given to the Riversleigh Project by: the Australian Research Grant Scheme (Grant PG A3 851506P); the National Estate Grants Scheme (Queensland); the Department of the Arts, Sport, the Environment, Tourism and Territories; Wang Australia Pty Ltd; ICI Australia Pty Ltd; the Queensland Museum; Ansett Wridgways Pty Ltd; the Australian Museum; the Australian Geographic Society; Mount Isa Mines Pty Ltd; and Surrey Beatty & Sons Pty Limited. Critical logistical support in field and laboratory was received from the Riversleigh Society, the Friends of Riversleigh, the Royal Australian Air Force, the Australian Defence Force, the Queensland National Parks and Wildlife Service, the Riversleigh Consortium (Riversleigh being a privately owned cattle station), the Mount Isa Shire, the Burke Shire, the Northwest Queensland Tourism and Development Board, the Gulf Local Development Association, PROBE, and many volunteer workers and colleagues - including Henk Godthelp who helped recover and prepare the specimen for study. Alan Rackham Snr and Alan Rackham Jnr discovered the "Terrace Site".

Dr R.E. Molnar, Prof. G. Grigg, Mr A. Wood, Mr H. Godthelp and Mr C. Manolis provided advice and suggestions or provided access to comparative material.

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NOTE ADDED IN PROOF:

A second fossil mandible of *Crocodylus johnstoni* (QM F17479) was located in the collections of the Queensland Museum by P. Willis. This mandible was found by M. Archer and H. Godthelp at 'Leichhardt 3', a locality on Floraville Station, on the Leichhardt River. The specimen is Late Pleistocene or post-Pleistocene in age (Godthelp, pers. comm.), so that the specimen described in the text of the paper probably represents the oldest known *Crocodylus johnstoni*. (R.E. Molnar.)